BREEDING SUCCESS AND NEST SITE CHARACTERISTICS OF THE RED-WINGED BLACKBIRD

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In many species of birds the process of nest site selection results in a general consistency in the qualitative characteristics of the nest site within particular habitats. It would seem that such consistency would have developed through a depression in reproductive success in those individuals acquiring nest sites of somewhat inferior quality. Within the normal range of nest site characteristics individuals acquiring nest sites with particularly advantageous characteristics or combinations of characteristics would be more successful reproductively than individuals not acquiring such sites. Selection would operate to maximize reproductive output by optimizing the nest site selection process.

The purpose of this study was to identify potentially important nest site characteristics of a species, to quantify these, and then to assess the relationships between these characteristics and reproductive success.

I selected Red-winged Blackbirds (*Agelaius phoeniceus*) for this study because: (1) their nesting habits provide a broad range of nest site characteristics which can be quantified; (2) they are colonial, thereby providing large numbers of nests within relatively small areas; (3) there is a considerable body of literature available on this species.

STUDY SITE AND METHODS

The study site was on a tidal salt marsh in southern Ocean County, New Jersey. Typically on these marshes, the lower elevations are dominated by 2 grasses (*Spartina alterniflora, S. patens*) which form expansive stands interrupted only by numerous potholes and creeks. At successively higher elevations, with concomitantly less tidal inundation, 3 shrub species appear that are used for nesting by Red-wings. These are, in order of increasing elevation, *Iva frutescens* (marsh elder), *Baccharis halimifolia* (sea myrtle), *Myrica pensylvanica* (bayberry). These shrubs generally are transitional between the low grass dominated marsh and the higher tree dominated upland areas. The study tract was along a dead end road that extends about 7 km onto the marsh. Because soil was added to the marsh surface in order to construct the road, this narrow strip of land is at a slightly higher elevation than the surrounding marsh. This increased elevation provides suitable habitat for the establishment of dense shrub stands along the edges of the road. It is in these roadside shrubs that the Red-wings nest.

I located, numbered, and subsequently observed nests through the course of the nesting season. Surveys were conducted on alternate days from 15 May–25 July 1973, with changes in nest conditions or contents assigned to the day intermediate to the visits. Nest site characteristics for each nest were measured following fledging of the young. These included nest height, total vegetation height at the nest, vegetation height

TABLE 1

COMPARISONS OF MEAN NEST SITE CHARACTERISTICS AMONG PLANT SPECIES USED AS NEST SUBSTRATE

Nest site characteristic	*Baccharis halimifolia* (78)[1]	*Iva frutescens* (106)	*Myrica pensylvanica* (13)
Vegetation height (cm)	179 (3.0)[2]	165 (2.2)	243 (7.5)
Nest height (cm)	135 (3.3)	112 (2.0)	182 (7.0)
Vegetation cover (cm)	44 (1.4)	54 (1.7)	61 (7.0)
% Cover	76.4 (1.57)	68.6 (1.27)	84.1 (4.50)

[1] Sample size.
[2] Standard error.

above the nest (vegetation cover) and distance to the nearest neighboring Red-wing nest. Since none of the nests was built in emergent aquatic vegetation, height measurements were made from ground level. To quantify the density of the vegetation over each nest I photographed the sky directly above the nest from the nest height using a 50 mm lens on a 135 mm single lens reflex camera. The negatives were projected onto a grid of 10 vertical and 10 horizontal lines. The 100 points resulting from the intersection of these lines composed the sample. The percentage of the total points covered by images of vegetation was taken as an index of vegetation density over the nest and is hereafter referred to as the percent cover. This process was repeated twice (each from opposite sides of the nest) for each nest with the mean value taken as the best estimate. Nest sites were mapped on aerial photographs of the study site and these were used to construct an index of nest density. For this I drew a circle including 1810 m^2 centered around each nest and used the number of nests included within that circle as the index. Because a number of nests and/or the supporting vegetation were lost or damaged before nest site characteristics could be measured, some nests could not be included in the analyses. The Student's *t*-test was used to analyze the results.

RESULTS

Breeding success and nest site characteristics.—Measurements of nest site characteristics are summarized in Table 1. These data are separated according to the plant species in which the nests were located. Comparisons among plant species for each nest site characteristic were significant in all but 2 cases. These exceptions occurred in vegetation cover between *Iva* and *Myrica*, and in percent cover between *Myrica* and *Baccharis*. Both comparisons involved *Myrica* for which there was a relatively small sample. In comparing the 3 plant species used as nest substrate, the relative magnitudes were the same for both vegetation height and nest height. The vegetation cover over the nest for the shortest shrub, *Iva frutescens*, was statistically indistinguishable from the tallest shrub, *Myrica pensylvanica*, but it was statistically greater than the intermediate shrub, *Baccharis halimifolia*. The percent cover for *Iva frutescens* was significantly less than the other 2 plant species which were not significantly different from each other. In *Iva*, which

Table 2

Breeding Success Relative to Nest Height

	Nest height (cm)										
	<100	100–109	110–119	120–129	130–139	140–149	150–159	160–179	180–199	>199	Total
No. nests	15	21	23	22	15	14	9	5	8	4	136
No. eggs	47	61	72	69	45	44	28	17	28	14	425
No. hatched	39	46	53	55	36	26	19	12	17	8	311
Hatched/egg	0.83	0.75	0.74	0.80	0.80	0.59	0.68	0.71	0.61	0.57	0.73
No. fledged	24	28	28	34	25	17	14	9	9	4	192
Fledged/hatched	0.62	0.61	0.53	0.62	0.69	0.65	0.74	0.75	0.53	0.50	0.62
No. successful nests	10	11	13	15	12	8	6	3	5	2	85
% successful	0.67	0.52	0.56	0.68	0.80	0.57	0.67	0.60	0.62	0.50	0.62

provides the least dense vegetation cover, nests were constructed further from the surface of the plant and closer to the ground than were nests in the other 2 shrubs.

I compared the relative levels of breeding success among nests in these 3 shrub species. There were no significant differences in clutch size, brood size, nor the number of young fledged per nest. Notwithstanding the rather distinctive nest site characteristics of the 3 shrub species used as nest substrate, there was no evidence that breeding success was related directly to any of these differences.

Nests were categorized according to the magnitude of each measured nest site characteristic. Ratios of the number of young hatched to the number of eggs laid (H/E) and the number of young fledged to the number of young hatched (F/H) within each category were used as an index to breeding success.

In Table 2 these indices along with the constituent data are presented relative to the height of the nest above the ground. There was a general decrease in the H/E ratio with increasing nest height. The F/H ratio increased steadily from the lower nest heights to the 160–179 cm nest height category after which breeding success decreased. A linear regression of the H/E ratio to nest height was significant (Fig. 1a); however, a simple relationship was not apparent for F/H ratio versus nest height (Fig. 1e).

The H/E ratio and vegetation height (Table 3) were negatively correlated indicating a general decline in hatching success with increasing vegetation height (Fig. 1b). There was, however, no obvious relationship between the F/H ratio and vegetation height (Fig. 1f).

Direct relationships between percent nest cover and nest density and the H/E and F/H ratios were not evident (Fig. 1c, d, g, h).

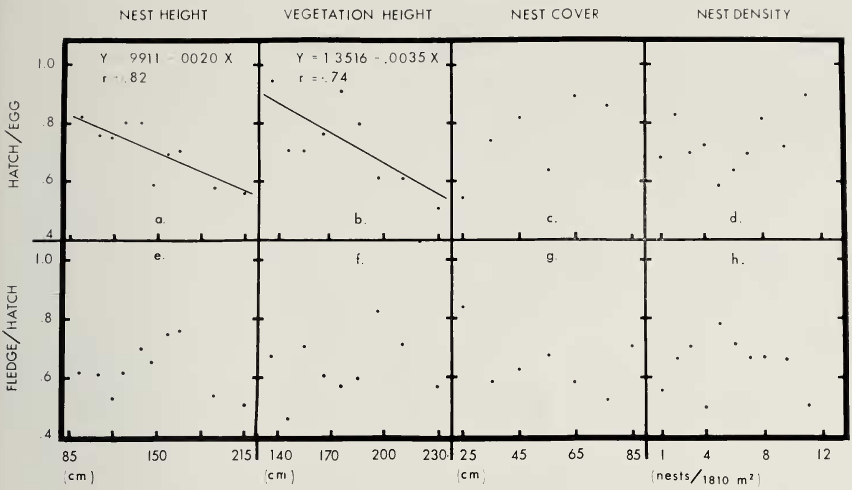

Fig. 1. Relationships between hatching and fledging success and nest site characteristics.

Mortality and nest site characteristics.—The 3 greatest sources of mortality to eggs and nestlings during this study were predation, abandonment, and death-in-nest (Caccamise 1976). Predation includes losses of both eggs and nestlings. Losses ascribed to abandonment include nest desertion and also apparent abandonment resulting from death of the adult. Losses from death-in-nest represent primarily nestling starvation, although a small percentage of losses in this category likely result from sources such as overcrowding

Table 3

Breeding Success Relative to Vegetation Height at the Nest

	Vegetation height (cm)									
	<140	140–149	150–159	160–169	170–179	180–189	190–199	200–219	>219	Total
No. nests	7	11	20	19	27	14	9	12	17	136
No. eggs	22	34	57	60	90	37	28	40	57	425
No. hatched	21	24	40	45	83	29	17	24	28	311
Hatched/egg	0.95	0.71	0.70	0.75	0.92	0.78	0.61	0.60	0.49	0.73
No. fledged	14	11	29	27	47	17	14	17	16	192
Fledged/hatched	0.67	0.46	0.72	0.60	0.57	0.59	0.82	0.71	0.57	0.62
No. successful nests	5	5	14	10	19	9	6	8	9	85
% successful	0.71	0.45	0.70	0.53	0.70	0.64	0.67	0.67	0.53	0.62

TABLE 4

COMPARISONS OF MEAN NEST SITE CHARACTERISTICS AMONG NESTS INCURRING MORTALITY (M) AND NESTS NOT INCURRING MORTALITY (S) FROM THE 3 GREATEST SOURCES OF NESTING MORTALITY

	Sources of Mortality								
	Abandonment			Death-in-nest			Predation		
Nest Site Characteristics	M(31)[1]		S(135)	M(48)		S(64)	M(39)		S(97)
Nest height (cm)	120	N.S.[2]	127	128	N.S.	123	136	N.S.	126
Vegetation height (cm)	174	N.S.	176	174	N.S.	176	185	*	173
Vegetation cover (cm)	53	N.S.	50	48	N.S.	50	50	N.S.	50
% Cover	72.7	N.S.	72.7	70.0	N.S.	70.5	75.5	N.S.	72.5
Distance to nearest nest (m)	15.3	N.S.	17.8	12.4	*	19.7	21.7	N.S.	16.4
Nest density (nests/1810 m^2)	4.8	N.S.	4.1	5.0	*	3.6	4.0	N.S.	4.2

[1] Sample size.
[2] Level of significance attained using Student's *t*-test; N.S. not significant; * significant at the 0.05 level.

and/or nest eviction. Since death-in-nest refers only to nestlings, those nests which did not successfully hatch young were not included in these comparisons.

For each nest site characteristic I compared nests incurring losses with those nests not incurring losses from each source of mortality (Table 4). Analyses indicated that nests incurring losses attributed to the death-in-nest category were characterized by a significantly smaller mean distance to the nearest nest and a significantly greater nest density. Also nests with losses to predators were in shrubs significantly taller than nests without such losses. None of the other comparisons were significant.

DISCUSSION

For the Red-winged Blackbird there have been many attempts to relate nest site characteristics to various measures of breeding success (Meanley and Webb 1963, Goddard and Board 1967, Holcomb and Twiest 1968, Robertson 1972, Holm 1973). In reanalyzing the nest height data from several of these studies and others, Francis (1971) found that some of the differences in breeding success, as related to nest height, were in fact not significant. He further suggested that the greater nesting success reported by Holcomb and Twiest (1968) in the higher nests, although significant, may have been related to differences in nest substrate rather than nest height.

In my study, nest site characteristics differed markedly for nests placed in the 3 plant species used as nest substrate. Additionally, as there were differences in the occurrence of the 3 shrub species according to the marsh elevation, the nests in these shrubs also reflected the differences in habitat distribution among the shrubs. However there were no detectable differences in breeding success among nests located in the 3 different plant species. Therefore it would seem that the differences in nest site characteristics specifically related to the differences in growth form among these plant species did not directly affect breeding success.

It is not clear why hatching success (H/E) decreased with increasing nest height and with increasing shrub height. Since nests incurring losses to predators were located in shrubs significantly taller than nests not receiving such losses (Table 4), it would appear that the nests in tall shrubs were more susceptible to losses to predators. While predation was not the only factor contributing to the differential hatching success, differences in predation pressure probably were important.

The reasons why relationships similar to those for hatching success did not apply between fledgling success (F/H) and nest height or vegetation height are obscure. However there is a major difference between eggs and nestlings in that eggs exhibit no behavior while nestlings do. Thus nestling behavior could affect predation as well as other sources of mortality.

Both measures of nest density indicated that nests incurring losses in the death-in-nest category were in areas of significantly greater nest density than nests not incurring such losses. In the current study the manifestation of nestling starvation was similar to descriptions of Red-wing nestling starvation appearing in the literature (Robertson 1973). Often starvation was noted initially when a nestling appeared somewhat smaller than its siblings, showing an increasing size disparity over a period of several days and eventually either disappearing or being found dead in the bottom of the nest.

At my study site territories of 1 to several females were maintained along the road borders in the dense stands of shrubs. Most foraging was done off the territories often along the numerous creeks and potholes common in the grass dominated areas of the marsh. It seems unlikely that the greater indices of nest density for nests incurring mortality from nestling starvation (Table 4) were related to overexploitation of food resources in high density areas. This is because the distance between areas of high nest density and low nest density was generally small compared to what might be considered the potential range in which a female could effectively forage. Orians (1961) pointed out that the amount of food obtained by a female on the territory is inversely related to the size of the territory; however, he also suggests that "it is doubtful whether food *per se* is the *proximate* factor by which territory size is regulated." Since nest dispersion at my study site was a linear array of nesting clumps along the road margin, each female had access to a large area of undefended marsh in which to forage. Considering the very large size of the foraging area relative to the number of Red-winged Blackbirds in this colony, it seems unlikely that food abundance would be significantly reduced only in the foraging areas used by females from areas of high nest density.

Alternatively, the one factor that always increases directly with nest density is the potential for intraspecific interactions in the vicinity of the nest. In areas of high nest density there would be considerable opportunity for such interactions while in areas of low nest density there would be very little opportunity. Female Red-winged Blackbirds, when in polygamous associations with a single male, will defend territories within the male's territory (Nero 1956; Nero and Emlen 1951). Thereby they exert an active role in determining the number of females able to breed in a specific territory (Orians 1961, Holm 1973).

Robertson's results (1973), indicating similar levels of starvation between low density upland areas and high density marsh areas, could be interpreted as mitigating against the possible role of aggression in nestling starvation. However, his results are based on averages over separate colonies or groups of colonies. Because these broad comparisons were designed to contrast habitat differences they ignore variations between individual nests. Such individual nest site characterizations are the basis for my study.

Since aggressive interactions between females seem to fill an important role in the mating system of the Red-winged Blackbird, excessive levels of aggression in areas of high nest density could impair the female's ability to nourish her young. Whether this would be sufficient to increase nestling starvation is open to conjuncture. However, the contribution of intraspecific aggression in determining breeding success certainly merits further study.

SUMMARY

Breeding success was assessed and nest site characteristics were measured in a colony of Red-winged Blackbirds nesting on a tidal salt marsh. Breeding success was not directly related to the plant species used as nest substrate, vegetation height over the nest, or density of cover over the nest. However, negative correlations were found between hatching success and both nest height and height of the shrub used as nest substrate. Nests incurring losses from nestling starvation were characterized as being in areas of significantly greater nest density than nests not incurring such losses. Also significant differences were evident in vegetation height between nests incurring predation and nests not incurring predation.

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